Bonn. zool. Beitr.	Bd. 45	H. 1	S. 17—31	Bonn, April 1994

A study of the baculum in the genus *Nycteris* (Mammalia, Chiroptera, Nycteridae) with consideration of its taxonomic importance

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Abstract. The bacula of 11 of the 15 species commonly recognised within the genus *Nycteris* (Cuvier & E. Geoffroy, 1795) have been examined. The bacula are described and illustrated, and notes on the systematics of the genus, with particular reference to bacular morphology, are included. *N. parisii* is considered distinct from *N. woodi* on the basis of bacular morphology. The baculum of *N. woodi* separates it from the other members of the *macrotis* group. *N. grandis* has a particularly distinctive baculum.

Key words. *Nycteris*, bacular morphology, systematics.

Introduction

The baculum (os penis) was first named by Thomas (1915). It is known to occur in five orders of Mammalia: Insectivora, Chiroptera, Primates, Carnivora and Rodentia and has been widely used in determining phyletic relationships, species diagnosis and as a criterion in age determination. Morphologically, it is one of the most diverse of all bones varying greatly among groups while staying more or less constant within species (Patterson & Thaeler 1982). It has played an important role in bat systematics both in discriminating between closely related, often sympatric species of which conventional morphological characters are otherwise very similar, such as *Myotis* and *Plecotus* and in determining taxonomic groupings such as in the Vespertilioninae; for a comprehensive study of this role in the Chiroptera see Hill & Harrison (1987).

The Nycteridae (Slit-faced bats) is a monogeneric family with a geographical range restricted to Africa, Arabia and south-east Asia (Hill & Smith 1984). As here understood it does not include New World taxa usually referred to *Lasiurus* (Gray 1831) but referred to *Nycteris* by Hall (1981) on account of nomenclatorial priority (see Anonymous 1929). As the name suggests, the Slit-faced bats are characterised by a deep median furrow margined by cutaneous lateral projections on the muzzle. The tail is enclosed throughout in the interfemoral membrane and is remarkable on account of the bifid form (T-shaped) of the last caudal vertebra. The ears are tall and rounded above and the tragus is well developed and simple in form. The skull has powerful supraorbital ridges with a postorbital process forming a frontal shield, which is deeply concave in the interorbital region. The premaxillaries are represented by palatal branches only. The dental formula is i 2/3 c 1/1 pm 1/2 m 3/3 = 32.

To date there has been no comprehensive review of the bacula of *Nycteris*, although Wassif & Madkour (1972) illustrated the baculum of *Nycteris thebaica*. Andersen (1912) undertook a brief review of the genus (which he referred to *Petalia*). He named eight new forms, recognised 15 valid species from Asia and Africa and divided them into four species groups: *javanica*; *aethiopica*; *hispida* and *thebaica*.

Ellerman & Morrison-Scott (1951) recognised two species in the Palaearctic and Indian regions, *N. javanica* and *N. thebaica* with the taxon *tragata* considered as a subspecies of *N. javanica* with a geographical range restricted to Burma, Malaysia and Borneo. Later (1955), they suggested that *N. tragata* was a distinct species on account of its apparently bifid upper incisors. In their review of Southern African mammals Ellerman et al. (1953) included a key, synonymies and a brief review of the geographical ranges of the six species which occur in the region: *N. nana*, *N. arge*, *N. hispida*, *N. thebaica*, *N. macrotis* and *N. woodi*. Aellen (1959) reviewed the four *Nycteris* species groups of Andersen (1912) and considered *N. javanica* to be distinct on account of its trifid upper incisors, and transferred the taxa *N. arge*, *N. nana* and *N. major* to a new group called the *arge* group; in consequence his five species groups were *arge*, *javanica* (restricted to Asia), *hispida*, *aethiopica* and *thebaica*. Subsequently Kulzer (1962) included *N. aethiopica* in the synonymy of *N. macrotis*. This view was not followed by Rosevear (1965) who recognised ten valid species in West Africa, including *N. aethiopica*, which he allocated to the same four African species groups as Aellen (1959). Rosevear included *N. parisii* in the *aethiopica* group, and the taxon *intermedia* was included in the synonymy of *N. arge*. Dalquest (1965) described *N. vinsoni*, which he considered to be closely related to *N. thebaica*, although a separate species. Kock (1969) regarded *N. gambiensis* as a subspecies of *N. thebaica* (a view followed by Koopman [1975]), and synonymised *N. vinsoni* with *N. macrotis*. Hayman & Hill (1971) recognised the same ten African species as Rosevear (1965) including *N. aethiopica*, and additionally including *N. woodi* from southern Africa. Following Rosevear (1965) they referred *N. intermedia* to *N. arge*. They suggested that *N. madagascariensis* probably represents *N. thebaica* "on the island". Koopman (1975) suggested that *N. aurita* could be a discrete species in East Africa, however for an alternative view see Harrison (1957). Like Kock (1969), Koopman (1975) considered *N. gambiensis* as a subspecies of *N. thebaica*. Honacki et al. (1982) listed 14 species worldwide (*N. arge*, *N. gambiensis*, *N. grandis*, *N. hispida*, *N. javanica*, *N. macrotis*, *N. madagascariensis*, *N. major*, *N. nana*, *N. parisii*, *N. thebaica*, *N. tragata*, *N. vinsoni*, *N. woodi*) maintaining *N. gambiensis* as a full species but including *N. aurita* in *N. hispida* (but see contrary views of Van Cakenberghe & De Vree [1993b]) and *N. aethiopica* in *N. macrotis*. Van Cakenberghe & De Vree (1985) undertook statistical analyses of the *macrotis* and *arge* groups; recognising *N. macrotis* and *N. woodi* in the former and *N. arge*, *N. nana*, *N. major* and *N. intermedia* in the latter. They considered *N. intermedia* as a distinct species, but recognised that the morphometric characters that discriminate it from *N. nana* and *N. arge* are "very faint", particularly versus *N. arge*. The taxon *madagascariensis* was included in the synonymy of *N. macrotis*; the taxon *parisii* could not be distinguished from *N. woodi* since the characters forearm length and pelage colour were inconclusive. Bergmans & van Bree (1986) stated that *N. tragata* was larger than *N. javanica* and suggested a need for further taxonomic investigations. Meester et al. (1986) included a full listing and classification of the southern African *Nycteris* with a key and distributions. Van Cakenberghe (1987), in a brief review of the genus, suggested that *N. javanica* was primitive and most closely related to the *arge* group. Corbet & Hill (1991) recognised 14 species (*N. arge*, *N. gambiensis*, *N. grandis*, *N. hispida*, *N. intermedia*, *N. javanica*, *N. macrotis*, *N. madagascariensis*, *N. major*, *N. nana*, *N.*

thebaica, *N. tragata*, *N. vinsoni*, *N. woodi*). They included *N. parisii* in *N. woodi* and treated *N. gambiensis*, *N. madagascariensis* and *N. vinsoni* as distinct species. Koopman (1992) considered *N. vinsoni* to be a subspecies of *N. macrotis*.

Materials and Methods

A combination of external, cranial and dental characters were used to identify the specimens which were taken from the collections of the Natural History Museum, London (BM) the Museum National d'Histoire Naturelle, Paris (MNHN), the National Museum of Zimbabwe (NM), and the Harrison Zoological Museum, Sevenoaks, Kent (HZM). Bacula were prepared from spirit specimens or dry study skins. Preparation involved light boiling followed by a period of maceration in a solution of 5 % potassium hydroxide and alizarin red stain followed by removal of the tissue by dissection. The cleared specimen was then stored in glycerol.

The figures were drawn using a Wild-Heerbrugg stereo microscope with attached camera lucida, and measured with a graticule scale. The same scale of magnification (x25) was used for all bacula, and the drawings provide dorsal (D) and right lateral (RL) views. The teeth and tragi were drawn at a magnification of x12. All drawings were by the senior author.

Results

Currently 15 species of *Nycteris* are recognised (Honacki et al. 1982; Corbet & Hill 1991), and their diagnostic characters are presented below (see Table 1). The four commonly recognised tragus types are illustrated in Fig. 1, and the posterior mandibular premolar form for each group is illustrated in Fig. 2. In total 48 bacula from 11 species were examined. Details of specimens, geographical range and bacular morphology are as follows:

Nycteris arge Thomas, 1903

Bacula examined: HZM.2.7845 (Zaïre); HZM.4.22620 (Congo); HZM.5.22621 (Congo); HZM.6.22622 [Fig. 3a] (Congo); HZM.7.22623 (Congo); HZM.8.23395 [Fig. 3b] (Congo).

Geographical distribution: Restricted to Africa; ranges from Sierra Leone to Zaïre and north-east Angola, Uganda, western Kenya, western Tanzania and south-western Sudan.

Bacular morphology: The baculum ranges from 3.15—4.28 mm in length. The shaft is long, slender, parallel-sided and essentially straight. The base is expanded and rounded; in lateral profile it is sometimes angled ventrally. The tip is simple, with only a small expansion.

Greatest length of bacula: 3.15 mm (HZM.2.7845); 4.28 mm (HZM.4.22620); 4.09 mm (HZM.5.22621); 3.75 mm (HZM.6.22622); 3.97 mm (HZM.7.22623); 4.10 mm (HZM.8.23395).

Nycteris intermedia Aellen, 1959

Bacula examined: No specimens were seen.

Geographical distribution: Restricted to Africa; including Ivory Coast; Ghana; Gabon; Cameroon; Angola; Liberia; Zaïre and Tanzania (after Van Cakenberghe & De Vree 1985).

Nycteris nana Andersen, 1912

Bacula examined: MNHN.1983—1030 (Cameroon); BM.22.12.17.37 [Fig. 3c] (Chiromo, Malawi); BM.54.794 (Congo).

Geographical distribution: Restricted to Africa; ranging from Ghana, Ivory Coast to north-east Angola and Zaïre; Uganda, western Kenya, south-western Sudan and western Tanzania.

Bacular morphology: The baculum ranges from 2.10—3.36 mm in length, smaller than that of *N. arge*. The shaft is slender, parallel-sided and essentially straight. As with *N. arge*, the base is expanded and rounded and in lateral profile is often angled ventrally. The tip is simple, with only a small expansion.

Greatest length of bacula: 3.36 mm (MNHN.1983—1030); 2.61 mm (BM.22.12.17.37); 2.10 mm (BM.54.794).

Nycteris major Andersen, 1912

Bacula examined: No specimens were seen.

Geographical distribution: Restricted to Africa; including Benin, Cameroon, Congo Republic, Gabon, south and east Zaïre.

Nycteris javanica E. Geoffroy, 1813

Bacula examined: MNHN.1948—491A (Java); MNHN.1948—491B [Fig. 3d] (Java); MNHN.1948—491C (Java).

Geographical distribution: Restricted to SE. Asia; ranges through Java to Bali.

Bacular morphology: The baculum is relatively shorter than that of *N. tragata* ranging from 2.76—2.88 mm in length. The shaft is long, slender, parallel-sided and essentially straight. The base is expanded and rounded and in lateral profile is angled ventrally. The tip is simple and expanded.

Greatest length of bacula: 2.88 mm (MNHN.1948—491A); 2.76 mm (MNHN.1948—491B); 2.85 mm (MNHN.1948—491C).

Nycteris tragata Andersen, 1912

Baculum examined: HZM.2.7442 [Fig. 3e] (Malaysia).

Geographical distribution: Restricted to SE. Asia; ranges from south Burma through Thailand, Malaysia, Sumatra and Borneo.

Bacular morphology: The baculum exceeds that of *N. javanica* in length. The shaft is long, slender and parallel-sided. The base is expanded and rounded, with a ventral angle in lateral view, as in *N. arge*. The tip is simple with only a small expansion.

Greatest length of baculum: 3.58 mm (HZM.2.7442).

Nycteris hispida Schreber, 1774

Bacula examined: HZM.4.2207 [Fig. 4a] (Kenya); HZM.27.4742 (—); HZM.28.4808 [Fig. 4b] (Cameroon); HZM.29.4809 [Fig. 4c] (Cameroon); HZM.32.4926 (Sierra Leone); HZM. 34.5645 [Fig. 4d] (Sudan); HZM.35.5646 (Sudan).

Geographical distribution: Restricted to Africa; ranging from Senegal to Somalia, Angola, Mozambique, Malawi, Zimbabwe and perhaps Namibia; Zanzibar; Bioko.

Bacular morphology: The baculum ranges from 3.33—4.16 mm in length. The shaft is long, slender and variably ventrally curved. The base is expanded and in lateral profile is angled ventrally. The tip is sometimes angled ventrally. It has a projection on the ventral aspect varying between individuals from a slight swelling to a pronounced hook.

Greatest length of bacula: 3.84 mm (HZM.4.2207); 3.97 mm (HZM.28.4808); 4.16 mm (HZM.29.4809); 4.03 mm (HZM.32.4926); 3.33 mm (HZM.34.5645); 3.33 mm (HZM.35.5646).

Nycteris grandis Peters, 1871

Bacula examined: HZM.2.2807 [Fig. 4e] (Kilosa, Tanzania); HZM.10.4716 [Fig. 4f] (Mikumi, Tanzania).

Geographical distribution: Restricted to Africa; ranging from Senegal to Zaïre, Kenya, Tanzania and Uganda to Zambia, Malawi, Zimbabwe and Mozambique; Zanzibar, Pemba. Possibly Namibia.

Bacular morphology: The baculum ranges from 3.45—3.54 mm in length, and is small in relation to body size. The shaft is stout and deep, unlike that of any other *Nycteris* examined. The base is narrow and in lateral profile is usually angled ventrally. The tip is squared, with a pronounced ventral projection.

Greatest length of bacula: 3.54 mm (HZM.2.2807); 3.45 mm (HZM.10.4716).

Nycteris macrotis Dobson, 1876

Bacula examined: HZM.2.1071 [Fig. 5a] (Somalia); HZM.3.2228 (Abakaliki, Nigeria); HZM. 6.3137 [Fig. 5b] (120 km north of Addis Ababa, Ethiopia); HZM.7.2634 [Fig. 5c] (Tanzania); HZM.16.2755 [Fig. 5d] (Tanzania); HZM.33.7158 (Tanzania); HZM.38.8952 [Fig. 5e] (Gambia); MNHN.1985—294 (Senegal).

Geographical distribution: Restricted to Africa; ranges from Senegal to Ethiopia, south to Zimbabwe, Botswana, Angola and Malawi; Zanzibar.

Bacular morphology: The baculum ranges from 3.84—5.12 mm in length, the longest in the study group. The shaft is long, parallel-sided and usually straight, thickening towards the base. The base has two basal lobes of varying development; in lateral view it is sometimes angled ventrally. The tip is expanded and trifid with three variably developed processes.

Greatest length of bacula: 4.42 mm (HZM.2.1071); 5.12 mm (HZM.3.2228); 3.84 mm (HZM.6.3137); 4.99 mm (HZM.7.2634); 4.67 mm (HZM.16.2755); 4.74 mm (HZM.33.7158); 5.06 mm (HZM.38.8952); 4.80 mm (MNHN.1985—294).

Nycteris parisii de Beaux, 1924

Baculum examined: BM.87.78 [Fig. 5f] (Somalia)

Geographical distribution: Restricted to Africa; including north Cameroon; southern Somalia and Ethiopia.

Bacular morphology: As in *N. macrotis*, the baculum is large in comparison to the other *Nycteris* studied. The shaft is long, parallel-sided and essentially straight, thickening towards the base. The base is expanded; in lateral profile it is angled ventrally. As in *N. macrotis*, the tip is expanded and trifid with three variably developed processes.

Greatest length of baculum: 4.30 mm (BM.87.78).

Nycteris woodi Andersen, 1914

Bacula examined: HZM.2.6696 (Masvingo, Zimbabwe); NM.60543 [Fig. 6a] (northern Mashonaland, Zimbabwe); NM.60545 [Fig. 6b] (northern Mashonaland, Zimbabwe); NM.60547 [Fig. 6c] (northern Mashonaland, Zimbabwe).

Geographical distribution: Restricted to Africa; including south-east Zimbabwe; central & eastern Zambia; south-west Tanzania.

Bacular morphology: The baculum ranges from 2.49—2.73 mm in length, one of the smallest of the study group. The shaft is straight and parallel-sided. The base is expanded; in lateral profile it is angled ventrally. The tip is simple and unexpanded, unlike *N. macrotis* and *N. parisii*.

Greatest length of bacula: 2.52 mm (HZM.2.6696); 2.73 mm (NM.60543); 2.49 mm (NM.60545); 2.49 mm (NM.60547).

Nycteris vinsoni Dalquest, 1965

Bacula examined: No specimens were seen.

Geographical distribution: Restricted to Africa; known only from Mozambique.

Nycteris thebaica E. Geoffroy, 1818

Bacula examined: HZM.122.5313 (Liwale, Tanzania); HZM.123.5314 [Fig. 7a] (Liwale, Tanzania); HZM.125.5340 [Fig. 7b] (Aden, south Yemen); HZM.129.5365 (South Africa); HZM.131.5367 (South Africa); HZM.154.6270 (Liwale, Tanzania); HZM.156.6293 (Liwale, Tanzania); HZM.157.6430 (Mwaya, Tanzania); HZM.160.6501 (Tanzania); HZM.161.6502 (Tanzania); HZM.165.7764 (Chilanga, Zambia).

Geographical distribution: Widespread; ranging from central and south western Arabia; Israel, Sinai, Egypt, Morocco, Senegal, Benin, Somalia and Kenya to South Africa; Zanzibar; Pemba.

Bacular morphology: The baculum ranges from 2.49—2.97 mm in length. The shaft is slender and parallel-sided. The base is expanded; in lateral profile it is usually angled ventrally. The tip is simple with a small expansion.

Greatest length of bacula: 2.91 mm (HZM.122.5313); 2.85 mm (HZM.123.5314); 2.69 mm (HZM.125.5340); 2.52 mm (HZM.129.5365); 2,70 mm (HZM.131.5367); 2.52 mm (HZM.154.6270); 2.49 mm (HZM.156.6293); 2.85 mm (HZM.157.6430); 2.73 mm (HZM.160.6501); 2.52 mm (HZM.161.6502); 2.97 mm (HZM.165.7764).

Nycteris gambiensis Andersen, 1912

Bacula examined: BM.56.35 [Fig. 7c] (Sierra Leone); BM.84.816 (northern Nigeria); MNHN.1984—1294 [Fig. 7d] (Senegal).

Geographical distribution: Restricted to Africa; including Senegal; Guinea; Sierra Leone; Ghana; Gambia; Togo; Upper Volta and Benin.

Bacular morphology: The baculum ranges from 2.88—3.42 mm in length. The shaft is slender and parallel-sided. The base is expanded and in lateral view is angled ventrally. The tip is simple with a slight expansion.

Greatest length of bacula: 2.88 mm (MNHN.1984—1294); 2.88 mm (BM.56.35); 3.42 mm (BM.84.816).

Nycteris madagascariensis Grandidier, 1937

Bacula examined: No specimens were seen.

Geographical distribution: Known only from Madagascar.

Discussion

The bacula of the eleven species of *Nycteris* studied fall into three basic morphotypes; in two the tip is trifid, *N. macrotis* and *N. parisii*; in two it is ventrally hooked, *N. hispida* and *N. grandis* and in seven it is simple, *N. arge*, *N. nana*, *N. tragata*, *N. javanica*, *N. thebaica*, *N. gambiensis* and *N. woodi*.

The baculum has proved to be a valuable additional character in distinguishing between certain species within the genus. In particular it shows that, contrary to views of Van Cakenberghe & De Vree (1985), *N. parisii* is a distinct species, not conspecific with *N. woodi* but more closely related to *N. macrotis*.

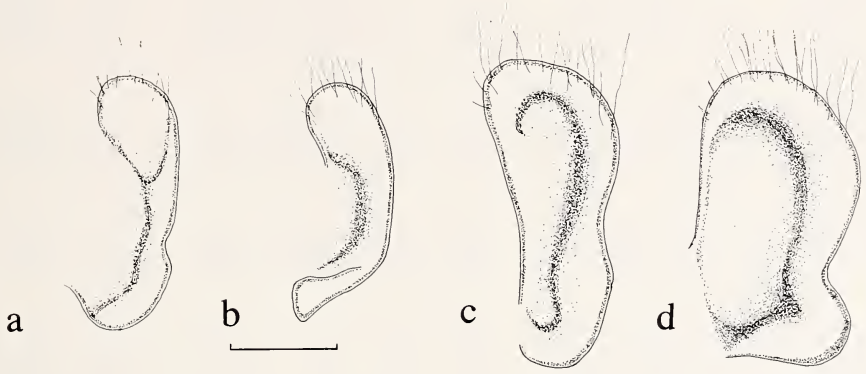

Fig. 1: Four tragus types found in *Nycteris*; (a) outer margin notched: *N. arge* (HZM.3.22619, Congo); (b) outer margin smooth: *N. hispida* (HZM.48.25092, Zimbabwe); (c) semi-lunate: *N. macrotis* (HZM.39.10127, Nigeria); (d) pyriform: *N. thebaica* (HZM.96.4910, Mozambique). — Scale = 2 mm.

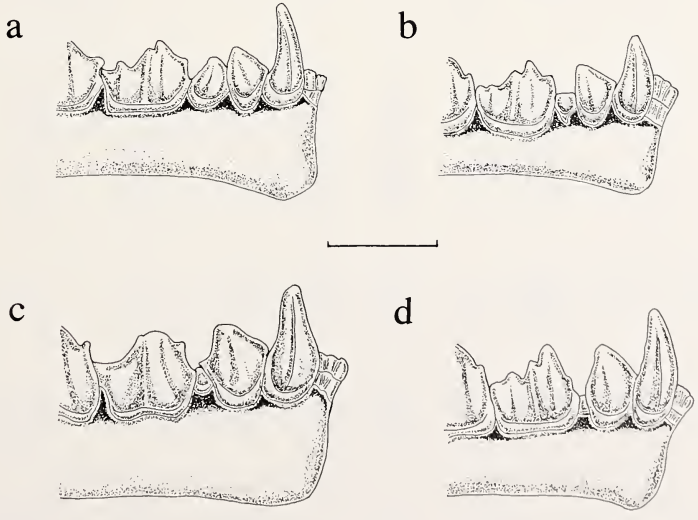

Fig. 2: Anterior mandibular dentition of *Nycteris*; (a) *N. arge* (HZM.6.22622, Congo); (b) *N. hispida* (HZM.33.5382, Tanzania); (c) *N. macrotis* (HZM.42.14215, Gambia); (d) *N. thebaica* (HZM. 125.5340, Arabia). — Scale = 2 mm.

Table 1: Character matrix of the fifteen species of *Nycteris* currently recognised.

Species	Forearm length (mm)	Ear length (mm)	Tragus shape	Posterior lower premolar form	Upper incisor form	Condylo-canine length (mm)	C—M³ (mm)	Bacular length (mm)	Bacular morphology
				arge group					
N arge	36.0—46.0*	28.0—33.0*	outer margin notched Fig. 1a	large Fig. 2a	bifid	16.4—18.1	6.2—7.6*	3.15—4.28	simple
N. intermedia	36.1—37.2*	23.5—24.0*	outer margin notched	large	bifid	GTL 17.6—18.7*	6.1—6.4*	—	—
N. nana	32.0—36.0*	20.0—22.0*	outer margin notched	large	bifid	13.8—14.2	5.0—5.8*	2.10—3.36	simple
N. major	47.0—50.0*	27.0—32.0*	outer margin notched	large	bifid	GTL 20.9—22.5*	7.0—7.8*	—	—
N. javanica	45.2—50.1	28.0—30.0	semi-lunate*	large	trifid*	17.6—19.5	7.0—8.3	2.76—2.88	simple
N. tragata	46.0*	28.5	outer margin smooth*	large	bifid*	16.5—19.4	6.8—8.1	3.58	simple
				hispida group					
N. hispida	36.0—45.0*	18.0—25.0*	outer margin smooth Fig. 1b	small Fig. 2b	trifid	13.8—16.2	5.4—6.5	3.33—4.16	ventrally hooked
N. grandis	57.0—66.0*	28.0—35.0*	outer margin smooth	small	trifid	22.5—24.4	8.2—9.9	3.45—3.54	ventrally hooked

Species	Forearm length (mm)	Ear length (mm)	Tragus shape	Posterior lower premolar form	Upper incisor form	Condylo-canine length (mm)	C—M³ (mm)	Bacular length (mm)	Bacular morpho-logy
				macrotis group					
N. macrotis	45.0—52.4*	28.0—36.0*	semi-lunate Fig. 1c	small Fig. 2c	bifid	18.0—19.8	6.8—8.2	3.84—5.10	trifid tipped
N. parisii	38.0—43.0*	19.2—21.0*	semi-lunate	small	bifid	14.9	5.6—6.0*	4.30	trifid tipped
N. woodi	37.0—42.5*	29.0—34.0*	semi-lunate	small	bifid	14.9—17.5	5.4—6.5	2.49—2.73	simple
N. vinsoni	50.0*	22.0*	semi-lunate*	small	bifid	CBL 22.0*	7.8*	—	—
				thebaica group					
N. thebaica	42.0—52.0*	28.0—37.0*	pyriform Fig. 1d	small Fig. 2d	bifid	16.4—18.3	6.0—7.0	2.49—2.97	simple
N. gambiensis	38.6—44.0*	21.0—34.0*	pyriform	small	bifid	15.9—16.7	5.0—6.5*	2.88—3.42	simple
N. mada-gascariensis	51.0*	27.0*	—	—	—	GTL 22.0*	8.0*	—	—

* Data from« Andersen (1912); Grandidier (1937); Aellen (1959); Dalquest (1965); Rosevear (1965); Hayman & Hill (1971); Adam & Hubert (1976); Van Cakenberge & De Vree (1985); Happold & Happold (1990); Koopman (1992).

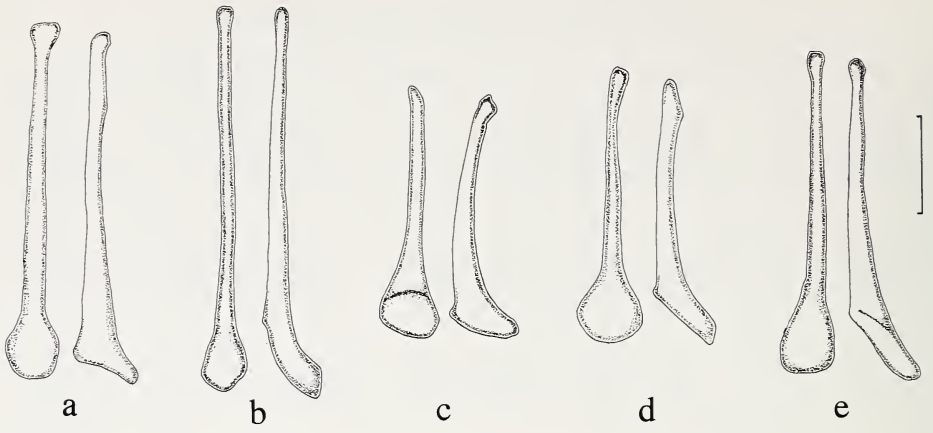

Fig. 3: Baculum (Dorsal [D] left; right lateral [RL] right of (a) *N. arge* (HZM.6.22622); (b) *N. arge* (HZM.8.3395); (c) *N. nana* (BM.22.17.37); (d) *N. javanica* (MNHN. 1948—491B); (e) *N. tragata* (HZM.2.7442). — Scale = 1 mm.

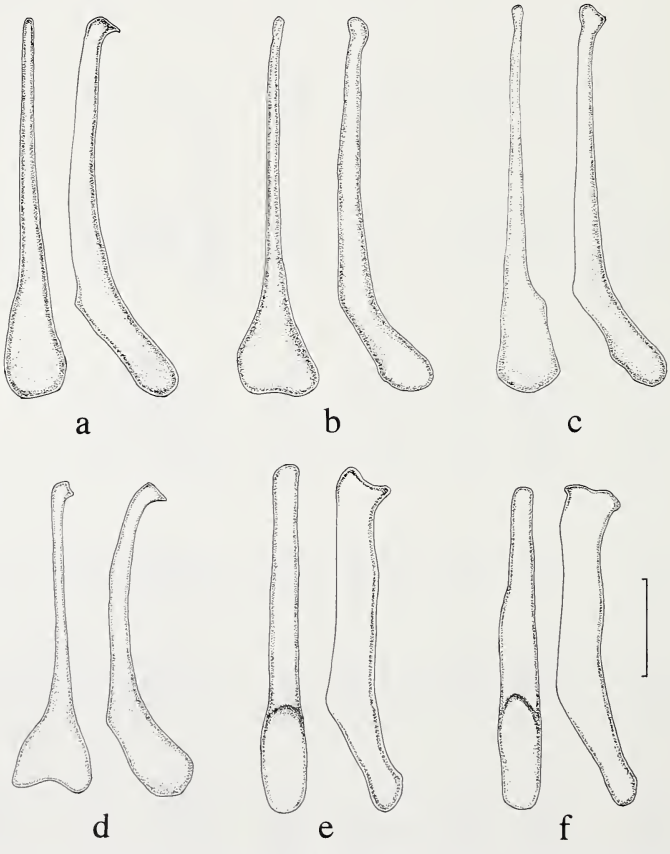

Fig. 4: Baculum (D, RL) of (a) *N. hispida* (HZM.4.2207); (b) *N. hispida* (HZM.28.4808); (c) *N. hispida* (HZM.29.4809); (d) *N. hispida* (HZM.34.5645); (e) *N. grandis* (HZM.2.2807); (f) *N. grandis* (HZM.10.4716). — Scale = 1 mm.

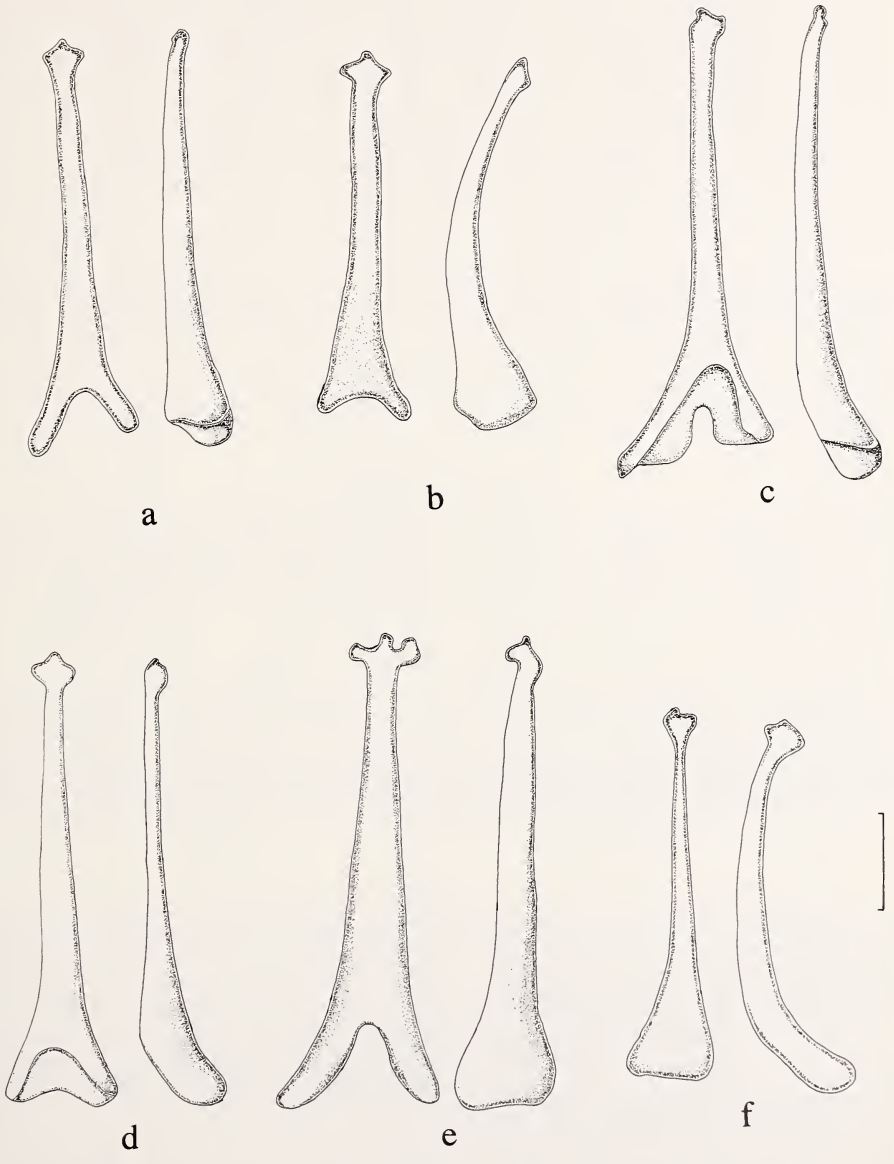

Fig. 5: Baculum (D, RL) of (a) *N. macrotis* (HZM.2.1071); (b) *N. macrotis* (HZM.6.3137); (c) *N. macrotis* (HZM.7.2634); (d) *N. macrotis* (HZM.16.2755); (e) *N. macrotis* (HZM.38.8952); (f) *N. parisii* (BM.87.78). — Scale = 1 mm.

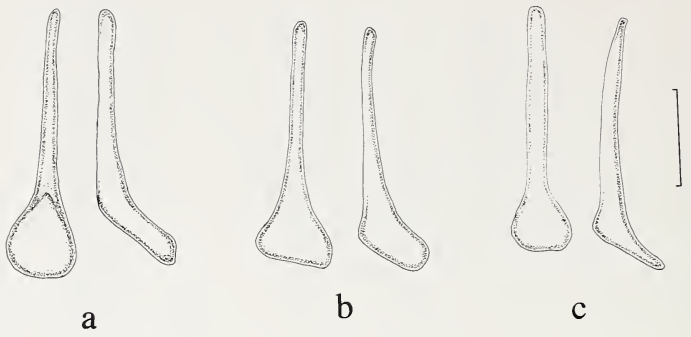

Fig. 6: Baculum (D, RL) of (a) *N. woodi* (NM.60543); (b) *N. woodi* (NM.60545); (c) *N. woodi* (NM.60547). — Scale = 1 mm.

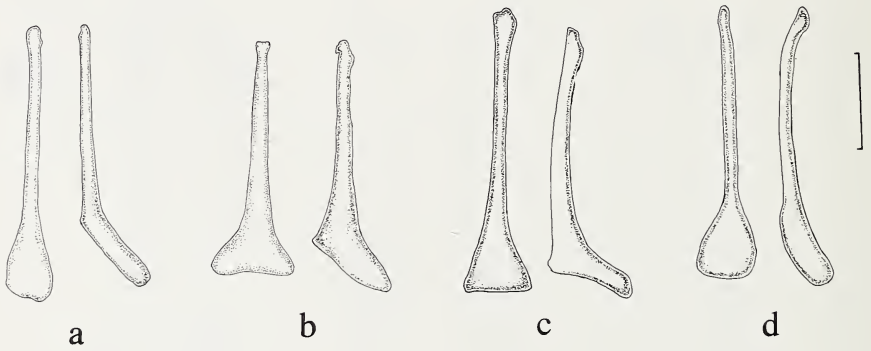

Fig. 7: Baculum (D, RL) of (a) *N. thebaica* (HZM.123.5314); (b) *N. thebaica* (HZM.125.5340); (c) *N. gambiensis* (BM.56.35); (d) *N. gambiensis* (MNHN.1984—1294). — Scale = 1 mm.

The baculum of *N. woodi* is the most simple of all the *Nycteris* studied. It clearly distinguishes this species from *N. macrotis*, the baculum of which has a trifid tip. This suggests that *N. woodi* may be less closely related to *N. macrotis* than previously thought, despite the parallel development of certain external and dental characters. *N. grandis* has a particularly distinctive baculum, with its narrow, deep base and shaft; this is not found in any of the other *Nycteris* species studied. Its ventrally hooked tip appears to support its relationship to the *hispida* group, in which a ventrally hooked tip is more or less apparent.

The baculum cannot be used to distinguish between the *arge* and *thebaica* groups. Within the *thebaica* group, the bacular morphology suggests that *N. thebaica* and *N. gambiensis* are closely related. It does not determine whether they are distinct species, the view of Rosevear (1965) or conspecific, the view of Kock (1969). Studies by Adam & Hubert (1976), Koopman et al. (1978), Koch-Weser (1984) and J. E. Hill (in litt.) indicate that two species are involved. Within the *arge* group it is interesting

to note that *N. javanica* and *N. tragata*, both isolated in south-east Asia, have a bacular morphology close to that of the other members of the group which are restricted to Africa. This supports the view of Andersen (1912) and Van Cakenberghe (1987) who included *N. javanica* and *N. arge* in the same group, but is contrary to that of Aellen (1959) and Van Cakenberghe & De Vree (1993a) who considered *N. javanica* to be distinct. The presence of *N. thebaica* in Arabia and the geographical separation of *N. javanica* and *N. tragata* from the rest of the *arge* group suggests that there have been at least two major dispersals of the genus in the Old World tropics. The first, possibly during a Miocene or Pliocene pluvial phase, saw the *arge* group disperse across forests which ranged uninterrupted from Africa to east Asia. Later, as climatically drier conditions prevailed, *N. javanica* and *N. tragata* became isolated in the mature forests of south-east Asia (Lekagul & McNeely 1977) whilst the rest of the *arge* group became restricted to the forests and woodlands of central and west Africa (Rosevear 1965). Meanwhile, *N. thebaica*, a species well adapted to more xeric conditions, extended its range from north-east Africa eastwards into Israel and southern and central Arabia, (Harrison & Bates 1991). It is curious that at present no species of *Nycteris* has been found in the Indian peninsula (Corbet & Hill 1992).

Acknowledgements

Many thanks are due to Woody Cotterill at the National Museum in Zimbabwe for all his help and support. We would also like to thank Paula Jenkins at the Natural History Museum, London, and Drs. Granjon and Cuisin at the Museum National d'Histoire Naturelle, Paris, for the generous loan of specimens. We are also most grateful to J. E. Hill for his valuable advice.

Zusammenfassung

Die Morphologie der Penisknochen (Bacula) wurde bei 11 der 15 bekannten Arten der Fledermausgattung *Nycteris* untersucht. Für jede Art werden Bacula abgebildet und beschrieben, und mögliche Konsequenzen für die Systematik der Gruppe werden diskutiert. *Nycteris parisii* wird aufgrund dieser Befunde als verschieden von *N. woodi* betrachtet. Das Baculum von *N. woodi* unterscheidet die Art auch von anderen Mitgliedern der *macrotis* Gruppe. *Nycteris grandis* zeichnet sich durch ein besonders charakteristisches Baculum aus.

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